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RESEARCH ARTICLE

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Genetic analysis of tolerance to aluminum toxin at seedling stage in soybean based on major gene plus polygene mixed inheritance model

Abstract The segregation analysis based on major gene plus polygene mixed inheritance model was employed to study the inheritance of aluminum (Al) tolerance in soybean. A recombinant inbred line (RIL) population derived from a cross between Al-tolerant (KF No.1) and Al-sensitive (NN 1138-2) parents along with both parents was analyzed using phenotypic data of three traits, i.e. relative total plant dry weight (RTDW), relative shoot dry weight (RSDW) and relative root dry weight (RRDW) assayed in sand culture. Significant difference among RILs was observed, and frequency distributions showed characteristics of mixed distributions, which suggested that inheritance of Al tolerance conformed to major gene plus polygene mixed inheritance model. The results indicated that the genetic model type I (four additive major genes plus additive polygenes) was the most fitting one for the traits, indicating some common genetic mechanism lying among the traits, though their respective best fitting models were somewhat different, i.e. I-6, I-9 and I-8 for RTDW, RSDW and RRDW, respectively, within model type I. It supports to choose RTDW as the representative for Al tolerance evaluation in addition to its virtue of being the whole-plant trait and easy to measure in sand culture. Averagely, the major genes contributed about 50%, while the collective polygenes contributed about 30% to the phenotypic variation, indicating both being important in breeding for Al tolerance. The study recommends that the segregation analysis can be used by soybean breeders who have accumulated abundant segregation data to obtain preliminary information on the inheritance of their breeding materials, and can be used as a first screening for presence of major genes followed with molecular marker analysis to further confirm and locate the major genes of quantitative traits.

Keywords soybean, aluminum tolerance, segregation analysis, major gene plus polygene mixed inheritance model, recombinant inbred line (RIL)

1 Introduction

Soybean is the world's most important modern-day food legume crop, supplying about 40% dietary proteins and 20% oil (Kauffman, 1987). As the world's demands for soybean products continue to rise, production acreages should be expanded and productivity improved. One of the constraints limiting soybean productivity is aluminum (Al) toxicity in acid soils, which accounts for about 40% of the world's arable lands (Aniol et al., 1980). Following absorption, Al damage in soybean results from accumulation of Al ions in the roots, stems and leaves causing root injury, leaf yellowing and stunted shoot growth, and finally reduced yields (Foy et al., 1992). Soil amendments such as lime application and irrigation can reduce soil acidity; however, they are costly, ineffective in subsoil and unsustainable especially in developing countries in the tropics and sub-tropics (Pandey et al., 1994). For these reasons, the development of Al-tolerant cultivars is a cost-effective strategy to these problem soils (Kochian et al., 2005).

To determine an appropriate indicator and suitable stage for evaluating tolerance of soybean cultivars to Al toxin is one of the keys to effective breeding for the trait. In the literature, relative dry weights of shoots and roots (Villagarcia et al., 2001), taproot length, surface area, lateral root (Gai et al., 2007) and an average membership

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index FAi (Qi et al., 2008) have been used in soybean. Korir et al. (2010) suggested to use relative total plant dry weight (RTDW) as the Al tolerance indicator due to its relatively better stability, higher correlation with other indicators and easier measuring procedure than the others with relative shoot dry weight (RSDW) and relative root dry weight (RRDW) recommended as reference indicators.

Although use of Al-tolerant cultivars in conjunction with soil management techniques has been adopted to improve productivity, it is necessary to identify genetic mechanisms that regulate Al tolerance to further enhance soybeans to acid soil environments (Spehar, 1995). Aluminum tolerance is a quantitative trait controlled by multiple genes and environment (Mackay, 2001). It is difficult to investigate, and therefore, inadequate knowledge of the relevant genetic mechanisms remains a challenge. Consequently, more research efforts are being put toward a better understanding of the genetic system of Al tolerance.

Describing the genetic model to understand the basis for Al tolerance may make it possible to breed tolerant cultivars for acid soils. Genetic analysis can be performed by segregation analysis (SA) procedure that utilizes phenotypic data to explore the inheritance of a quantitative trait. It is considered as a first choice method for plant breeders with only phenotype data at hand, and this is especially true when acquisition of molecular data is expensive, labor-intensive and limited in usage. In the study of the inheritance of quantitative traits in plants, Gai and Wang (1998) developed a procedure of SA that utilizes information of one or multiple segregating populations with their parents based on the principles of major-gene plus polygene mixed inheritance model. Here, the gene with a large effect performs as the major gene, while the gene with a relatively small effect performs as the minor gene or polygene (Gai et al., 2003).

The mixed inheritance model for complex traits in plants has been applied in the genetic study of plant quantitative traits such as maturity, tofu quality, oil content, cyst nematode resistance and foliar feeding insect resistance in soybean, bacterial blight and wide compatibility in rice, maturity in rapeseed and dwarf mosaic virus resistance in maize with their results published in more than 200 articles (Wang and Gai, 2001; Gai et al., 2003; Gai, 2006). Recently, the analytical procedures of three major genes plus polygenes mixed inheritance model have been expanded to four major-genes plus polygene mixed inheritance model that fits DH and RIL (Wang et al., 2010), and the joint segregation analysis method for the four generations P_1, P_2, F_1 and RIL has been set up.

In the present study, our objective was to describe the genetic system of Al tolerance in soybean based on major gene plus polygene mixed inheritance model since little information about the mixed inheritance model of Al tolerance in soybean was known.

2 Materials and methods

2.1 Materials

The plant materials used were the recombinant inbred line (RIL) population NJRIKY with 184 F_2: 7-derived lines from a cross between KF No.1 (Al tolerant) and NN 1138-2 (Al sensitive) by using the single-seed descent method. Previous studies showed that the two parents exhibited contrasting characteristic for Al tolerance (Gai et al., 2007; Qi et al., 2008) and other agronomic traits (Zhang et al., 2004).

2.2 Experiments carried out and measurement of Al-tolerance indicators

The RIL population with both parents was assayed at a young seedling stage for Al tolerance in pot sand culture under greenhouse conditions in summer 2006 and 2007 at Jiangpu Station, Nanjing Agricultural University, China. Al tolerance was evaluated under Al-stress (480 μM) versus Al-free (0 μM) following the procedure of Villagarcia et al. (2001) with minor modifications. A split-plot-like experimental design with the two Al levels as main plots and RILs and parents as subplots was employed with three replications in each of the seasons. Plants were thinned to three per pot 7 d after emergence and treated for 14 d before data collection. Shoots and roots from each treatment pot were separated and dried to a constant weight at 65°C for 48 h and then weighed. Total plant dry weight was determined as the sum of shoot and root dry weights, and Al-tolerance was defined as growth (dry weight basis) in Al-stress relative to its control (Al-stress/Al-free). Thus, the Al-tolerance indicators evaluated were relative dry weight of total plant (RTDW), shoot (RSDW) and root (RRDW).

2.3 Method of segregation analysis

The joint segregation analysis method for RIL population based on four major genes plus polygene mixed inheritance model (Wang et al., 2010) was used for data analysis. The meanings of major gene plus polygene mixed inheritance model include the following points: (1) A quantitative trait may be controlled by multiple genes with different effects, large or small not necessary equal. (2) The gene with large effect performs as the major gene, while the gene with relatively small effect, which cannot be detected in the experimental conditions, performs as the minor gene or polygene. (3) The distinction between major and minor genes is relative to and depends on the experimental error or precision, and under one environment, a gene may perform as a major gene, while in another environment, as minor one(s). (4) A gene may perform as a major gene under a precise experiment, while

it cannot be detected individually and may perform as minor one(s) under a less-precise experiment. Therefore, for a quantitative trait, the genetic system with both major and minor gene(s) is a general model, and pure major gene genetic system and pure minor gene genetic system are only specific cases to the general model. The underlying genetic assumptions are diploid nuclear inheritance with no maternal or cytoplasmic effects, no interaction or linkage between major genes and polygenes, and no selection; the polygene effect and the environment effect in segregating population follow a normal distribution; and the variances within the two homozygous parents and the F_1 populations are equal.

Five main points or steps in the basic procedures of the segregation analysis under major gene plus polygene mixed inheritance model are as follows: (1) The frequency distribution of a segregating population is composed of several component distributions of major gene genotypes. Each component meets the assumption of normality and is modified with both polygenes and environments. Therefore, the whole distribution is a mixture of several components meeting the assumption of normality. (2) The maximum likelihood function is established from a single segregating generation or jointly from multiple generations. In the function, the proportion, mean, and variance of each component distribution are included and are to be estimated from the experimental data. Eight types of genetic models, one major gene model (A), two major gene model (B), polygene model (C), one major gene plus polygene model (D), two major gene plus polygene model (E), three major gene model (F), three major gene plus polygene model (G), four major gene model (H), and four major gene plus polygene model (I) are considered. In each type, there are several models regarding the existence of the additive, dominance, and epistasis effect of major gene and polygene in various segregating generations. (3) EM algorithm is used to estimate the number of component distributions in a mixture distribution. For a better convergence, the iterated ECM (IECM) algorithm is used, in which the E step is the same as in the EM algorithm, while the conditional maximization (CM) step is composed of two to three CM parts. The iteration is taken continuously to obtain a set of stable and consistent results. (4) After the maximum-likelihood analysis of all types of genetic models for a given set of experimental data are conducted, the Akaike's Information Criterion (*AIC*) and a set of tests, including uniformity test, Smirnov test, and Kolmogorov test, are used to choose an optimal genetic model and pick up its corresponding estimates of component distributions. (5) The estimates of genetic parameters, including the additive, dominance, and epistasis effects of major gene(s), the total additive, dominance, and epistasis effects, and heritability of major gene, and the heritability of polygene, are calculated from the estimates of component distributions of the optimal genetic model by using the method of least squares according to the relationship between the genetic parameters and the component distribution parameters of a given model. The detailed procedures and formulae are omitted here and can be referred to Wang et al. (2010).

3 Results

3.1 Frequency distribution of Al tolerance in the population

The frequency distributions of Al-tolerant traits showed the characteristic continuous variation of quantitative traits (Table 1). The data confirmed that between the two parents, KF No.1 (P_1) was tolerant and NN1138-2 (P_2) was sensitive to Al toxin. Variation in each trait in the RIL population was generally somewhat wider than the value of parents, especially the larger values were greater than that of the tolerant parent, and most families concentrated near the mid-parent values. Heritability values were estimated as 77.8%, 74.3% and 80.5% for RTDW, RSDW and RRDW, respectively, indicating that all had high efficiency for phenotypic selection of the traits. The histograms in Fig. 1 showed that the RIL distributions were composed of component distributions that indicated the inheritance of Al tolerance conformed to the major gene plus polygene mixed inheritance model and composed of several component distributions of major gene genotypes. Therefore, the data were suitable for segregation analysis based on the major gene plus polygene inheritance model (Gai, 2006).

The Al tolerance indicators RTDW, RSDW and RRDW revealed significant difference in genotypes and showed low error variances (Table 2). However, RTDW was chosen as the preferred indicator to describe the genetic model for Al tolerance in this study due to its relatively better stability and easier measuring procedure than the others, but also analyzed the other two component traits.

Table 1 Frequency distribution of Al-tolerance traits in (KF No.1 × NN 1183-2)RIL population

trait/%	class interval										mean	range	*GCV*/%	h^2/%
	50.0–54.9	55.0–59.9	60.0–64.9	65.0–69.9	70.0–74.9	75.0–79.9	80.0–84.9	85.0–89.9	90.0–94.9	sum				
RTDW	0	2, P2	24	51	29	39	29, P1	7	3	184	73.1	56.3–93.9	12.7	77.8
RSDW	0	1	14,P2	46	42	23	28	23, P1	7	184	75.2	59.6–93.3	11.9	74.3
RRDW	1	13, P2	24	58	37	24	15, P1	8	4	184	70.9	52.9–94.5	13.8	80.5

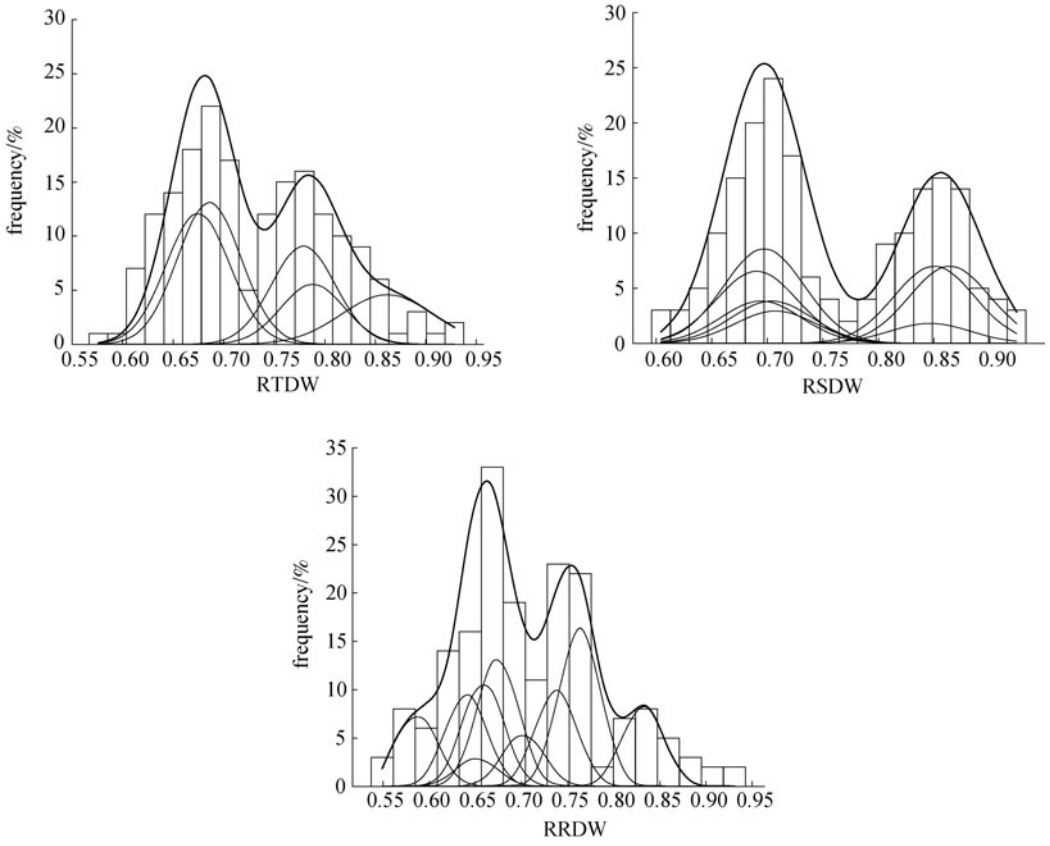

Fig. 1 Distribution of RTDW, RSDW and RRDW of (KF No.1 × NN 1183-2) RIL population

Note: Histogram represents sample distribution; curve lines represent fitted theoretical distribution of the population and respective component distributions under the major gene plus polygene mixed inheritance model. The best-fitting genetic model for the traits was model I (four major genes plus polygenes mixed inheritance model).

Table 2 ANOVA of Al-tolerance traits

source of variation	*df*	*MS*		
		RTDW	RSDW	RRDW
replication	2	0.114**	0.084**	0.1649**
RIL	183	0.017***	0.019***	0.0199***
error	366	0.001	0.001	0.0012
total	551			

3.2 Selection of inheritance model fitting Al tolerance

The data were fitted with the A, B, C, ... and I model types by using the maximum-likelihood method and the IECM algorithm. The best fitting model was selected according to *AIC* values, the maximum-likelihood ratios (*MLH*) and a set of goodness-of-fit tests. Table 3 showed the first selected four best models for each indicator from all kinds, all types of possible models, in which two best models with highest *MLH* and lowest *AIC* values for each trait were further selected for goodness-of-fit tests (Table 4). Finally, the model that performed better in goodness-of-fit tests was chosen as the best fitting model for each indicator, and then its genetic parameters were estimated.

Table 3 The values of maximum likelihood and Akaike's information criterion of the candidate models

trait	model	model code	*MLH*	*AIC*
RTDW	**F-4**	**MG3-2EA**	**158.22**	**−311.45**
	I-1	MX4-AI PG-AI	137.71	299.42
	I-6	**MX4-4EA PG-A**	**149.31**	**−316.61**
	I-9	MX4-3EA PG-AI	144.68	301.37
RSDW	H-3	MG4-4EA	139.65	295.29
	H-4	MG4-2EA	131.90	277.79
	I-6	**MX4-4EA PG-A**	**143.35**	**−304.70**
	I-9	**MX4-3EA PG-AI**	**144.85**	**−301.69**
RRDW	C-0	PG-AI	412.88	205.16
	I-2	MX4-AI PG-AI	98.98	221.97
	I-8	**MX4-2 × 2EA PG-A**	**147.39**	**−317.03**
	I-10	**MX4-3EA PG-AI**	**151.52**	**−304.78**

Note: MG: Major gene model; MX: Mixed major gene and polygene model; PG: Polygene model; A: Additive effect; I: additive × additive epistasis; EA: Equal additive. For example, model I-8 = MX4-2 × 2EA PG-A means major gene plus polygene mixed model with 2 sets of 2 major genes of equal additive effect plus polygenes with additive effects.
Boldface indicates the models selected for further goodness of fit tests.

Table 4 Test for goodness of fit of the fitted models for Al-tolerant traits

trait	model	generation	U_1^2	U_2^2	U_3^2	${}_nW^2$	D_n
RTDW	F-4	P_1	5.1337(0.0235)	6.6374(0.0100)	2.3408(0.1260)	0.0600(>0.05)	0.6164(>0.05)
		P_2	8.7936(0.0030)	3.7491(0.0528)	13.9871(0.0002)	0.1635(>0.05)	0.9905(>0.05)
		RIL	0.5878(0.4433)	1.4624(0.2265)	19.8793(0.0000)	3.8003(<0.05)	0.9044(>0.05)
	I-6	**P_1**	**4.1118(0.0777)**	**4.7835(0.0287)**	**0.8012(0.3707)**	**0.7425(>0.05)**	**0.5888(>0.05)**
		P_2	**1.7724(0.1831)**	**3.7489(0.0528)**	**13.8851(0.0002)**	**0.1625(>0.05)**	**0.9893(>0.05)**
		RIL	**0.0089(0.9248)**	**1.4545(0.2278)**	**3.4894(0.0618)**	**3.0333(<0.05)**	**0.8917(>0.05)**
RSDW	I-6	P_1	6.3838(0.0115)	9.2478(0.0024)	5.6576(0.0174)	0.0605(>0.05)	0.6429(>0.05)
		P_2	5.9076(0.0151)	3.4493(0.0633)	3.9385(0.0472)	0.0645(>0.05)	0.8368(>0.05)
		RIL	3.8556(0.0496)	12.0146(0.0005)	39.1878(0.0000)	3.8333(<0.05)	0.8713(>0.05)
	I-9	**P_1**	**3.2742(0.0692)**	**4.6736(0.0306)**	**0.8585(0.3542)**	**0.0625(>0.05)**	**0.5375(>0.05)**
		P_2	**5.1009(0.0239)**	**3.2479(0.0715)**	**2.3666(0.1240)**	**0.0725(>0.05)**	**0.7879(>0.05)**
		RIL	**2.2051(0.1376)**	**0.5528(0.4572)**	**7.7132(0.0055)**	**3.8333(<0.05)**	**0.8825(>0.05)**
RRDW	**I-8**	**P_1**	**1.9137(0.1666)**	**2.0093(0.1563)**	**0.0975(0.7549)**	**0.0625(>0.05)**	**0.5644(>0.05)**
		P_2	**8.6489(0.0033)**	**3.7436(0.0530)**	**13.3275(0.0003)**	**0.0625(>0.05)**	**0.9997(>0.05)**
		RIL	**1.9982(0.1575)**	**5.2418(0.0221)**	**13.5663(0.0002)**	**3.8333(<0.05)**	**0.9398(>0.05)**
	I-10	P_1	1.6856(0.1942)	2.0132(0.1559)	0.4188(0.5175)	0.0625(>0.05)	0.6420(>0.05)
		P_2	8.0173(0.0046)	3.6982(0.0545)	10.7197(0.0011)	0.0625(>0.05)	0.9993(>0.05)
		RIL	14.2736(0.0002)	19.7407(0.0000)	9.8592(0.0017)	3.8333(<0.05)	0.9290(>0.05)

Note: Boldface indicates the models selected finally as the best fitting models of the respective traits.

On this basis, F-4 (three but two equal additive major gene model) and I-6 (four equal additive major gene plus additive polygene model) with *AIC* of −311.45 and −316.61, respectively, were the two best possible fitting models for RTDW since *AIC* values were not obviously different (Table 3). The tests of goodness-of-fit (Table 4) showed that model I-6 had more values with larger probability among the five tests and, thus, was considered the optimal model for this trait. Compared to major genes of model F-4, the four major genes of model I-6 could be due to three genes with major effects (as in F-4) and a fourth gene of smaller effect.

For RSDW, models I-6 (four equal additive major gene plus additive polygene model) and I-9 (four equal additive major gene plus additive epistasis polygene model) were possible fitting ones. Both their *MLH* (143.35, 144.85) and *AIC* (−304.70, −301.69), respectively, were not obviously different, but in the test of goodness-of-fit, I-9 passed most of the tests for most generations and, thus, was chosen as the optimal model.

The fitting models for RRDW were I-8 (four but two equal additive major gene plus additive polygene model) and I-10 (four but three equal additive major gene plus additive polygene model). The *AIC* for I-8 (−317.03) and I-10 (−304.78) were not obviously different, but *AIC* for I-8 was lower. Goodness-of-fit tests showed model I-8 had more values of higher probability for various tests, especially on the RIL generation that showed segregation information about alleles in parents. Model I-8 was thus considered optimal.

From the above model fitting procedure, RTDW, RSDW and RRDW were all controlled by four major genes plus polygenes where the former contributed a major part and the latter contributed about two thirds of the former to the total phenotypic variation, indicating that they shared very similar genetic mechanism and that both major genes and polygenes should be utilized in breeding for Al tolerance.

3.3 Estimates of genetic parameters

Estimates of first-order and second-order genetic parameters of the best fitting model of each trait are presented in Table 5. Four major genes with equal additive effect plus polygenes with additive effect (Model I-6) controlled RTDW. The additive effect of major genes was estimated as 0.073, and that of collective polygenes was estimated as 0.015. The estimated results of second-order genetic parameters showed that major genes explained 54.6% while polygenes accounted for 30.2% of total phenotypic variation in the population, indicating in the genetic constitution of RTDW major gene being important, but polygene also played an important role.

Similar situation was for the other two traits, but briefly, 4 major genes with three equal additive effect plus polygenes with additive and epistasis (Model I-9) controlled RSDW. The additive effects of major genes were estimated as three positive equal additive effects of 0.028 and one negative additive effect of −0.026, respectively. The collective additive effect and epistasis of polygenes were estimated as 0.013 and 0.026,

respectively. The major genes explained 49.4%, while polygenes accounted for 28.8% of total phenotypic variation.

Table 5 also showed that for RRDW, the model of 4 major genes with 2 sets of 2 equal additive effects plus polygenes with additive effect (Model I-8) was chosen as the best fitting model. Among the four major genes, two had equal positive additive effect of 0.060, and two others had equal negative effect of −0.020. Its collective polygene effect was estimated as 0.032. The major gene and polygene explained 41.7% and 26.2% of phenotypic variation, respectively.

From the above results, it was implicated that the genetic effects of major genes were quite different among the traits, even though the three indicators were all fitting the model type I. In RTDW, the positive alleles were from the tolerant parent KF No.1 with equal effect; in RSDW, the 3 positive alleles were from KF No.1, while another was from sensitive parent NN1138-2; and in RRDW, the two large positive alleles were from KF No.1, while the two small negative alleles were from NN1138-2. On the other hand, the collective polygene effects were also different among the three indicators, especially collective epistatic effect that existed in RSDW. These results indicate the different genetic constitutions among the indicators.

4 Discussion

The detection of major genes for quantitative traits is a topic of intensive research by both biologists and plant breeders. Aluminum tolerance is an important quantitative trait for selection of soybean genotypes for acid soil environments. Our previous study (Korir et al., 2010) suggested to use RTDW as the major Al tolerance indicator due to its relatively better stability, higher correlation with other indicators and easier measuring procedure than the others, with RSDW and RRDW recommended as reference indicators. The results of the present study showed the three indicators followed a same model type I of the four major gene plus polygene mixed inheritance model, indicating some common genetic mechanism lying among them, though their respective best fitting model was somewhat different within model type I. Therefore, this conclusion supports the choosing of one indicator as the representative to be used in Al tolerance evaluation, and RTDW is the appropriate one due to its virtue of being the whole-plant trait and easy to measure in sand culture.

The present results showed that for Al tolerance, the major genes contributed about 50%, while the collective polygenes contributed about 30% of the phenotypic variation. It implies that in breeding for Al tolerance, not only major genes but also polygenes are important, and both should be converged through genetic operation by traditional and molecular breeding procedures. However, the breeding procedures of pyramiding major genes are commonly available, but the procedures to pyramiding both are still to be further explored.

The mixed inheritance model of major genes and polygenes adapted from segregation analysis (Gai et al., 2003) provides an efficient way to analyze the inheritance of complex traits. As the present study indicated, the major gene effects could be estimated, while the rest of individual minor gene effects would be merged into the collective polygenic effects, showing that the model provides more genetic information in contrast to the traditional Mendelian genetic analysis. The segregation analysis, therefore, can be easily used by plant breeders who have accumulated abundant segregation data to get some preliminary information on the inheritance of their breeding materials, and also can be considered as the first screening for presence of major genes (and gene effects) that control quantitative traits followed with molecular marker analysis to further confirm and locate the major genes.

5 Conclusions

The genetic model type I (four additive major genes plus additive polygenes) was the most fitting one for Al tolerance traits, RTDW, RSDW and RRDW, indicating some common genetic mechanism lying among the traits, though their respective best fitting models were somewhat different, i.e. I-6, I-9 and I-8, respectively, within the model

Table 5 Estimates of genetic parameters of the best fitting model for each trait

model	trait	first order genetic parameters estimates		second order genetic parameter estimates					
		m	gene effect	σ_p^2	σ_e^2	σ_{mg}^2	σ_{pg}^2	h_{mg}^2 (%)	h_{pg}^2 (%)
I-6	RTDW	0.692	$d_a = d_b = d_c = d_d = 0.073$	0.0055	0.0008	0.0030	0.0017	54.6	30.2
			$[d] = 0.015$						
I-9	RSDW	0.689	$d_a = d_b = d_c = 0.028$; $d_d = -0.026$	0.0063	0.0014	0.0031	0.0018	49.4	28.8
			$[d] = 0.013$; $[i] = 0.026$						
I-8	RRDW	0.590	$d_a = d_b = 0.060$; $d_c = d_d = -0.020$	0.0199	0.0064	0.0083	0.0052	41.7	26.2
			$[d] = 0.032$						

Note: m: population mean; d_a, d_b, d_c, d_d: additive effect of the major genes; $[d]$: collective additive effect of polygenes; $[i]$: collective epistatic effect of polygenes; σ_p^2: phenotypic variance; σ_{mg}^2: major gene variance; σ_{pg}^2: polygene variance; h_e^2: environmental variance; h_{mg}^2 (%): major gene heritability; h_{pg}^2 (%): polygene heritability.

type. Accordingly, RTDW was chosen as the representative of the Al tolerance traits in addition to its virtue of being whole-plant trait and easy to measure in sand culture. The major genes contributed averagely about 50%, while the collective polygenes about 30% to the phenotypic variation, and, therefore, both should be important in breeding for Al tolerance in soybean.

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